

Impacts of invasive stream salmonids on native fish: using meta-analysis to summarize four decades of research

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Received 5 Jan. 2010, accepted 29 Apr. 2010 (Editor in charge of this article: Outi Heikinheimo)

Korsu, K., Huusko, A. & Muotka, A. 2010: Impacts of invasive stream salmonids on native fish: using meta-analysis to summarize four decades of research. *Boreal Env. Res.* 15: 491–500.

Salmonid fishes are among the most frequently introduced organisms. We included 58 papers to meta-analysis to assess the effects of introduced stream salmonids on native salmonids. We also explored whether the responses of native species depended on the type of study. Introduced salmonids had negative effects on the foraging rate, abundance and survival of native salmonids, which also altered their habitat use in the presence of invaders. Brown trout appeared to be the ‘worst’ alien species (strongest impact on native fish). Negative effects were most pronounced when several introduced species were present. Moreover, the magnitude of the impact was related to the study type: the observed impacts were stronger in laboratory streams than in field enclosures or in natural streams. Our results indicate that introduced salmonid species may have little effect on native fish in some areas, but may have substantial effects in other parts of their range.

Introduction

Introduction and establishment of species beyond their natural ranges is one of the major threats to biodiversity, being second only to habitat loss and fragmentation (Sala *et al.* 2000). Although the impacts of alien species on recipient ecosystems and native organisms are often negative, not all introductions are detrimental; in fact, Williamson (2006) suggested that only a minor portion of species introductions are likely to cause detectable changes to native ecosystems. Exotic species also provide a unique opportunity to understand ecological and evolutionary processes at relevant spatial and temporal scales (Sax

et al. 2007). It is therefore a great challenge to conservation biologists to distinguish *a priori* introductions that are likely to be detrimental to native biodiversity.

Because of their economical and societal value, stream-dwelling salmonids are among the most frequently introduced fish species, being now established on many continents (Rahel 2007). Outside their native ranges, salmonids have had harmful effects on native ecosystems, including agonistic behaviour towards, and hybridization with, the native species, and population fragmentation and decline of the natives. Furthermore, community-wide impact of introduced salmonids that alter not only freshwater,

but also riparian ecosystems, have been reported (Simon and Townsend 2003, Baxter *et al.* 2004). Due to multiple adverse effects, two of the salmonid species — brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) — rank among the eight fish species included in the list of 100 of the world's worst invasive alien species (Lowe *et al.* 2000). Therefore, fisheries managers around the world have launched extensive management programs to control salmonid invasions, and possibly eradicate already established populations, with the aim of conserving native fish populations (Novinger and Rahel 2003, Jackson *et al.* 2004, Finlayson *et al.* 2005).

The impacts of alien salmonids on native fish have a long history of scientific documentation, yet only a few papers have attempted to identify general patterns in salmonid invasions (but see Krueger and May 1991, Dunham *et al.* 2002, Fausch 2008, Korsu *et al.* 2008). Even these few are narrative and somewhat case-specific, and are not focused on the detection of general impacts of alien salmonids on native fish, particularly other salmonids. Therefore, the mechanisms facilitating invasions, and potentially resulting in the reduction of regional distinctiveness and loss of native biota, are not well understood. Two major mechanisms that have been proposed are: (i) niche pre-adaptations facilitates invaders' establishment in their introduced ranges (e.g. Fausch *et al.* 2001, Korsu *et al.* 2007); and (ii) invaders displace native salmonids through aggressive behaviour (e.g. DeWald and Wilzbach 1992, Wang and White 1994).

Here, we use a meta-analysis to quantify the impacts of alien salmonids on their native counterparts. We summarize the effects of introduced salmonids on the behaviour, habitat use, growth, abundance and survival of native salmonids, comparing the responses of native species in allopatry to those in sympatry with the introduced species. Because the presence of multiple invaders tends to weaken the biotic resistance of the recipient system (Hewitt and Huxell 2002), we also examined whether the magnitude of the impact was greater when several species were introduced. Moreover, we examined whether the three most extensively introduced salmonids — brown trout, brook trout (*Salvelinus fontinalis*)

and rainbow trout — differ in their impacts on native salmonids. Finally, because patterns may be greatly modified by the scale of observations (e.g. Underwood *et al.* 2005), we explored whether the responses of the native species to invader presence differed between studies conducted at widely variable spatial scales and using different methodological approaches (laboratory channels, fish enclosure designs and field studies). We hypothesized that studies forced to restricted spatial scales could intensify interspecific interactions, reducing the native species' performance and potentially resulting in stronger effect sizes.

Material and methods

We used a meta-analysis to assess the general effects of introduced stream salmonids on the vital rates, behaviour and habitat use of native salmonids. We conducted a thorough literature search on studies published between 1970 and January 2008 using ASFA (Aquatic Sciences and Fisheries Abstracts) and Google Scholar™, supplemented with our own reference collections. We also added our own unpublished material to this data set which thus comprised 58 studies (Table 1). We divided the studies in six groups based on the response variables measured: aggression, habitat use, foraging, growth, survival, and abundance. We further divided the habitat use data according to the five most frequently measured responses: use of stream pools, focal position (vertical distance from stream bed), and use of cover, depth, and water velocity. In a majority of experimental studies, fishes were of similar size and age (mostly age-0 or age-1) or reflected the size structure in the field during the experiment (e.g. Taniguchi *et al.* 2002). Since a preliminary analysis indicated no age-related differences in response variables, we did not consider fish age in further analyses.

We included all studies that provided (i) an estimate of the mean and (ii) the number of replicates in both sympatric and allopatric situations. The number of aggression was usually measured only in sympatric (alien vs. native) trials to test whether agonistic acts were targeted mainly toward the native species. In this subset,

Table 1. The list of studies included in the meta-analysis. Shown are the species involved and the geographical area of each study. Species are: arctic grayling (AG, *Thymallus arcticus*), Atlantic salmon (AS, *Salmo salar*), brook trout (BKT, *Salvelinus fontinalis*), bull trout (BLT, *Salvelinus confluentus*), brown trout (BRW, *Salmo trutta*), chinook salmon (CKS, *Oncorhynchus tshawytscha*), coho salmon (CS, *Oncorhynchus kisutch*), cutthroat trout (CTT, *Oncorhynchus clarki*), dolly varden (DV, *Salvelinus malma*), masu salmon (MS, *Oncorhynchus masou*), rainbow trout (RT, *Oncorhynchus mykiss*), and white-spotted charr (WSC, *Salvelinus leucomaenis*). The code refers to the type of analysis for which data from each study were used: a = abundance, g = growth, f = foraging, h = habitat, i = interaction (aggression, dominance), s = survival.

Authors	Native species	Nonnative species	Area	Code
Baldigo and Lawrence 2000	BKT	BRW	North America	a
Baxter <i>et al.</i> 2004	DV	RT	Japan	a, g
Beall <i>et al.</i> 1989	AS	CS	North America	g, s
Blanchet <i>et al.</i> 2007a	AS	RT	North America	g
Blanchet <i>et al.</i> 2007b	BRW	RT, BKT	Europe	s
Blann and Healey 2006	CS, CTT	AS	North America	g, i
Budy <i>et al.</i> 2007	CTT	BRW	North America	g, s
Byorth and Magee 1998	AG	BKT	North America	g, h
Cunjak and Green 1984	BKT	RT	North America	i
Cunjak and Power 1986	BKT	BRW	North America	h
De la Hoz Franco and Budy 2005	CTT	BRW	North America	a
De Staso and Rahel 1994	CTT	BKT	North America	i
DeWald and Wilzbach 1992	BKT	BRW	North America	g, f, h, i
Fausch and White 1981	BKT	BRW	North America	h
Fausch and White 1986	BKT	BRW, CS	North America	g
Griffith 1972	CTT	BKT	North America	h, i
Gunckel <i>et al.</i> 2002	BLT	BKT	North America	g, f, h, i
Hasegawa and Maekawa 2006	WSC, MS	BRW, RT	Japan	h
Hasegawa <i>et al.</i> 2004	WSC, MS	BRW, RT	Japan	i
Hearn and Kynard 1986	AS	RT	North America	h, i
Hephworth <i>et al.</i> 2001	CTT	BKT, BRW	North America	a
Isely and Kempton 2000	BKT	RT	North America	g
Jones and Stanfield 1993	AS	RT, CS, BRW	North America	g, s
Korsu <i>et al.</i> 2007	BRW	BKT	Europe	a
K. Korsu unpubl. data*	BRW	BKT	Europe	g, h, i
Larson and Moore 1985	BKT	RT	North America	a
Larson <i>et al.</i> 1995	BKT	RT	North America	a
Levin <i>et al.</i> 2002	CKS	BKT	North America	s
Lohr and West 1992	BKT	RT	North America	h
Magoulick and Wilzbach 1998	BKT	RT	North America	a, g, h
McGrath and Lewis 2007	CTT	BKT	North America	a
McHugh and Budy 2005	CTT	BRW	North America	g
McHugh and Budy 2006	CTT	BRW	North America	g, s
McMahon <i>et al.</i> 2007	BLT	BKT	North America	f, g, i, s
McRae and Diana 2005	BKT	BRW	North America	a
Moore <i>et al.</i> 1983	BKT	RT	North America	a
Morita <i>et al.</i> 2004	WSC	RT, BRW	Japan	a, h
Nakano <i>et al.</i> 1998	BLT	BKT	North America	f, h
Peterson <i>et al.</i> 2004	CTT	BKT	North America	a, s
Platts and Nelson 1988	BLT, CTT	BKT, BRW	North America	a
Quist and Hubert 2005	CTT	BKT, BRW	North America	a
Rahel and Nibbelink 1999	BKT	BRW	North America	a
Rieman <i>et al.</i> 2006	BLT	BKT	North America	a
Rodtka and Volpe 2007	BLT	BKT	North America	f, g, i
Rose 1986	BKT	RT	North America	g
Scott <i>et al.</i> 2003	AS	CKS	North America	s
Scott <i>et al.</i> 2005	AS	CKS	North America	i
Seiler and Keeley 2007	CTT	RT	North America	f, i
Shemai <i>et al.</i> 2007	CTT	BRW	North America	g
Shepard <i>et al.</i> 2002	CTT	BKT	North America	a
Shepard 2004	CTT	BKT	North America	a
Taniguchi <i>et al.</i> 2002	MS	RT	Japan	f, g, i, s
Volpe <i>et al.</i> 2001	RT	AS	North America	f, g, i
Wang and White 1994	CTT	BRW	North America	i
Waters 1999	BKT	BRW, RT	North America	a
Weigel and Sorensen 2001	BKT	BRW, RT	North America	a
Whitworth and Strange 1983	BKT	RT	North America	a
Yrjänä 2003	BRW	BKT	Europe	a

* The results were published after January 2008 (see Korsu *et al.* 2009, 2010).

we included also two papers (Cunjak and Green 1984, Hasegawa *et al.* 2004) that reported the achieved dominance status in two-fish trials (as a proportion of dominant to subordinate individuals). To measure the effects on native species' abundances, we used values from manipulative (removal) experiments, natural 'experiments' (allopatric vs. sympatric conditions in the field), as well as documented invasions (before-after data). In some cases, true allopatry was hard to define because of, for example, incomplete removal of the alien species (e.g. Peterson *et al.* 2004). We, therefore, used a 10% density threshold to categorize a site as allopatric or sympatric. For studies reporting abundance responses by the native fish, we also tested for the impact of introducing multiple alien species compared with single-species introductions. Because introduced species often rearrange the community rather than simply enter an empty slot (Herbold and Moyle 1986), we hypothesized that the magnitude of the impact should be greater when several species were introduced. This hypothesis is supported by recent theoretical evidence showing that strong biotic resistance only occurs when the invasion process is restricted to a single species, whereas the presence of multiple invaders tends to weaken the resistance (Hewitt and Huxell 2002).

Next, we compared the species-specific impacts of three salmonid species: brown trout, rainbow trout, and brook trout. We chose these species because the two first-mentioned are included in the list of 100 of the world's worst invasive alien species (Lowe *et al.* 2000). Brook trout, although extensively transferred from its original range in eastern North America to other parts of the continent, as well as to other continents, is often referred to as a relatively harmless intruder with little impact on native species (Vooren 1972, Blanchet *et al.* 2007a, Hesthagen and Sandlund 2007). However, an increasing number of studies indicate harmfulness of this species for recipient systems (Dunham *et al.* 2002, Spens *et al.* 2007, Korsu *et al.* 2007). For these three species, we calculated effect sizes (see below) by including all response variables in a single categorical meta-analysis to demonstrate the general impact of these species on native salmonids.

We calculated effect sizes for each study as the logarithmic response ratio, $\ln R$, where R refers to values in sympatry (treatment) divided by those in allopatry (control) (see Rosenberg *et al.* 1997). Thus, negative values of $\ln R$ mean that, for the native species, the value of a response variable was lower in sympatric than allopatric situations, indicating a negative impact of the alien species on the native one. However, as there was generally no means of deciding *a priori* whether a certain habitat shift was harmful to a native species, we considered all habitat shifts caused by the invader harmful (e.g. to either shallower or deeper stream positions); thus, habitat use is presented as negative (or zero) $\ln R$ values only. For aggression, we calculated $\ln R$ only for sympatric trials, with negative $\ln R$ indicating that the alien species dominated and/or expressed more aggression towards the native species. For all effect size calculations, we used study means weighted by the number of replicates (Rosenberg *et al.* 2000). This was done because, in many cases, treatments were unreplicated, or the study was pseudoreplicated (for example, multiple sampling sites in one stream), thus not allowing us to compute study-specific standard deviations. We calculated 95% bias-corrected bootstrap confidence intervals for $\ln R$ (4999 permutations). All calculations were made using the MetaWin 2.0 software (Rosenberg *et al.* 2000). This procedure partitions the total heterogeneity for a particular comparison (Q_T) into within-group (Q_w) and between-group (Q_b) components. Means were considered to be significantly different from zero if bootstrap confidence intervals did not overlap zero.

We further examined whether the magnitude of the alien impact depended on the study type. For this purpose, we divided the studies based on whether they were conducted in (i) laboratory channels, (ii) fish enclosures in natural streams or semi-natural outdoor channels, or (iii) natural streams (both broad-scale removal experiments and natural 'experiments' included). We hypothesized that studies using restricted spatial scales could intensify interspecific interactions, reducing the native species' performance and potentially resulting in stronger effect sizes. However, as many studies have shown that the growth of a native salmonid may be either suppressed or enhanced by the presence of an alien fish (e.g.

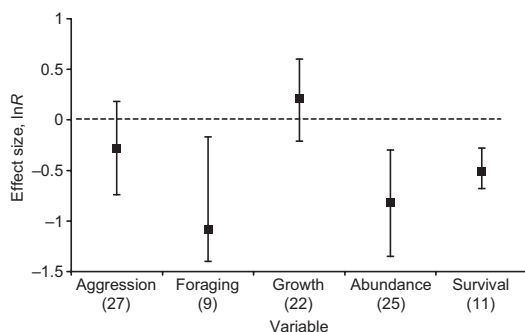


Fig. 1. Mean effect sizes ($\ln R$) with 95% bootstrap confidence intervals for the five response variables (number of studies in parentheses). Negative values indicate a negative impact of the alien salmonid on native salmonids.

Volpe *et al.* 2001, Blann and Healey 2006, Blanchet *et al.* 2007b), we analysed growth separately from other response variables (survival, foraging, and habitat use combined).

Results

Studies of salmonid invasions in streams show a strong geographical bias: a great majority of studies come from North America ($n = 49$), while only a few studies have been conducted in Europe ($n = 4$) or Japan ($n = 5$) (Table 1). The harmful impact of alien salmonids on the native ones was most clearly demonstrated by the negative effect sizes on the foraging rate, abundance and survival, while no effects were detected for aggression or growth (Fig. 1). Fish habitat use, particularly use of cover and water depth, was also modified by the invader (Fig. 2).

Brown trout was by far the 'worst' alien salmonid (i.e. had the strongest impact on native fish), while rainbow trout and brook trout had similar and only weakly negative impacts on native salmonids ($Q_B = 27.82$, $p < 0.0001$) (Fig. 3). Furthermore, the effect on native fish abundance was most pronounced when more than one alien fish were present: with one alien, $\ln R$ was -0.40 (bootstrap confidence intervals: -1.06 to 0.06 , $n = 14$), whereas it was -1.15 (-1.75 to -0.95 , $n = 8$) in systems with at least two alien salmonids ($Q_B = 12.24$, $p < 0.001$).

The magnitude of the impact was related to study type, with much stronger impact in

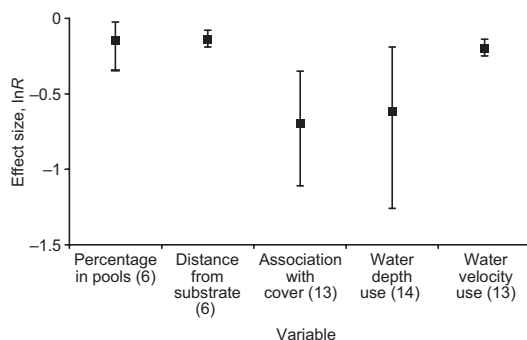


Fig. 2. Mean effect sizes ($\ln R$) with bootstrap confidence intervals for habitat use. For other explanations, see Fig. 1.

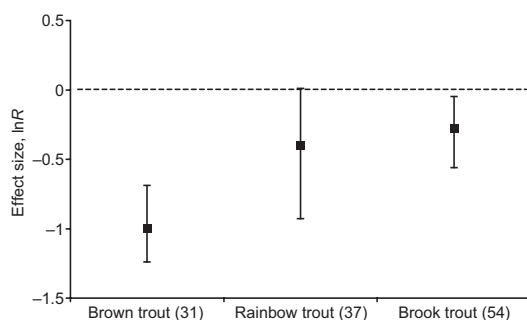


Fig. 3. Mean effect sizes ($\ln R$) with bootstrap confidence intervals (all variables combined) for the impact of three salmonid species in their introduced ranges. For other explanations, see Fig. 1.

spatially restricted laboratory channels as compared with that in more natural settings (survival, foraging, and habitat use combined: $Q_B = 13.74$, $p < 0.001$, Fig. 4a; growth: $Q_B = 7.90$, $p = 0.019$, Fig. 4b). The growth response was slightly, though non-significantly positive (CI overlapped zero), but only in studies conducted in laboratory channels (Fig. 4b). For other variables, the impact was negative, regardless of the methodology and the study scale (Fig. 4a).

Discussion

Our results showed that introduced stream salmonids, especially brown trout, have diverse negative effects on native salmonids. Especially habitat use, foraging rate, abundance, and survival were modified by the aliens. Moreover,

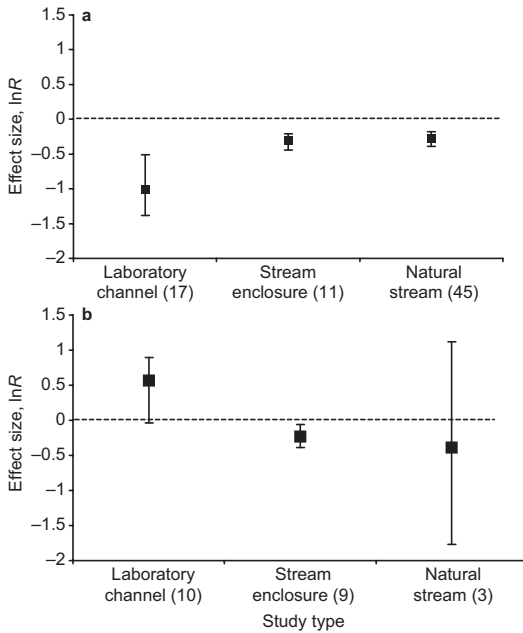


Fig. 4. Mean effect sizes ($\ln R$) with bootstrap confidence intervals for (a) survival, foraging, and habitat use (combined), and (b) growth according to study type. Length of study sections in each category was (mean \pm 1SE): laboratory channels 8.2 m (\pm 1.6, range 0.3–16 m), enclosures 55.8 m (\pm 25.7, range 1.3–300 m), and natural stream reaches 863 m (\pm 366.9, range 20–4300 m). For other explanations, see Fig. 1.

populations of the native species were severely reduced in streams supporting more than one introduced species. The magnitude of the impact was also affected by the methods used, with laboratory studies reporting the strongest impacts.

Our meta-analysis comprised studies from North America, Europe and Japan, with a great majority being conducted in North America where salmonids have been extensively transferred across the continent. Our data do not allow a rigorous assessment of pattern similarity between continents, but the adverse impacts of alien salmonids are clearly not unique to North America: similar effects have been reported in South America (Rodríguez 2001), Japan (e.g. Taniguchi *et al.* 2002) and Europe (Korsu *et al.* 2007), reinforcing the generality of our findings. Furthermore, the impacts of introduced salmonids may even be stronger if the recipient habitat does not contain any closely related native fish (i.e. native species are naïve to the introduced

species; see Cox and Lima 2006). For example, in New Zealand, the introduced brown trout have caused extensive population fragmentation and endangerment of native galaxids (Townsend and Crowl 1991), as well as strong cascading impacts on stream food webs (Nyström *et al.* 2003).

According to the enemy release hypothesis, alien species benefit from having left their old enemies (predators, competitors, and parasites) behind, while native species continue to struggle against their co-evolved, natural enemies (Sax and Brown 2000, Shea and Chesson 2002). Our results lend indirect support to this hypothesis, because the same species were often reciprocally aliens and natives, depending on the direction of introductions and the recipient salmonid guild. For example, brook trout is native in eastern North America where its populations are reduced by both rainbow and brown trout (Krueger and May 1991, Fausch 2008). However, in the native ranges of these two invaders, the introduced brook trout meet only limited biotic resistance, allowing their establishment and spread, with sometimes severe impacts on native trout (Benjamin *et al.* 2007, Korsu *et al.* 2007, Fausch 2008).

The negative effects of introduced fish on native species' abundances were most pronounced in streams with more than one introduced species. This finding supports niche-based explanations of invasion success: the more alien species there are, the less empty niche space is available, forcing the native species to adjust to biologically modified environments with multiple new competitors (see Davis 2003). It is also possible that an increased number of introduced species may create positive feedback cycles that cause the effects of invaders to rapidly accumulate over time, a phenomenon called 'invasion meltdown' (Simberloff 2006). Interestingly, studies examining the impact of multiple alien species are rare, particularly if compared to the large body of literature addressing the role of species richness in preventing invasions (e.g. Shea and Chesson 2002, Hierro *et al.* 2004, Levine *et al.* 2004).

The magnitude of the impact also depends on the identity of the species introduced, with brown trout being the worst invader of the three species examined. Interestingly, rainbow trout and brook

trout appeared to be equally bad, although only the former one is included in the list of 100 of the world's worst invasive alien species (Lowe *et al.* 2000), while the latter species is often considered a harmless invader (Vooren 1972, Blanchet *et al.* 2007a, Hesthagen and Sandlund 2007). It thus appears that interactions among native and alien salmonids are highly context-dependent, varying in relation to case-specific factors such as characteristics of the species involved and the recipient environment (Fausch 2008, Korsu *et al.* 2008, Ricciardi and Kipp 2008). Furthermore, methodological issues are also involved: impacts appeared much stronger in laboratory settings than in stream enclosures or reach-scale observational studies. While this may hint to a laboratory artifact, it might also reflect a scaling problem, with the strongest effects being observed in spatially restricted laboratory streams. The impact of the alien species at small spatial scales is not necessarily negative, however: in fact, the growth of the native species in laboratory tanks was on average higher in the presence than absence of an invader. While this finding may also be a scaling artifact, it has indeed been suggested that growth facilitation among two fish species, one native, the other one introduced, might in fact take place through behavioural stimulation (Blann and Healey 2006). A whole suite of methodological approaches from laboratory and field experiments to observational studies at multiple spatial scales are needed to resolve mechanisms of alien species impact on native salmonids (*see also Dunham et al.* 2002).

The role of aggressive behaviour to salmonid invasion success is often postulated, because stream salmonids typically use agonistic acts to establish social hierarchies and maintain energetically optimal feeding positions (Fausch 1984, DeWald and Wilzbach 1992, Wang and White 1994). Our results, however, gave no support for aggression as the driving force for the superiority of introduced salmonids. Indeed, Korsu *et al.* (2007) showed that brook trout, a species regarded as relatively non-aggressive (DeWald and Wilzbach 1992), has invaded across the native range of the more aggressive brown trout in North European streams. Thus, it is likely that other factors, operating beyond direct interference, regulate salmonid invasions in streams.

It is also possible that, if competition is important, it is so only during certain periods of time (e.g., immediately after hatching; Rose 1986) and in relatively homogenous, non-fluctuating environments where the invaders may establish through a 'hostile takeover' (*sensu* Melbourne *et al.* 2007, Korsu *et al.* 2010). As an interesting parallel, Sax *et al.* (2007) suggested that research on biotic resistance should change focus from competition-based explanations to more comprehensive consideration of other biotic interactions such as predation and pathogens. Being notoriously variable and disturbance-prone environments (e.g. Lake 2000), streams can be expected to produce constantly new niche opportunities for exotic species, with little need to invoke competition-related explanations.

Despite considerable context-dependency, our analyses do provide some evidence for general patterns in salmonid invasions. Adverse effects were detected for both individual- and population-level variables, potentially driving native fish to the brink of extinction. An important implication from our study is that introductions of alien salmonids beyond their natural ranges almost certainly incur a high risk of negative impacts on native biota. Therefore, if no prior information on the impacts of alien salmonids is available, it is preferable to avoid introductions altogether rather than being forced to costly and unreliable eradication measures after the harm has already been done. This is even more so because species considered harmless to native fish in some areas (e.g. brook trout in southern Europe; Blanchet *et al.* 2007a) may cause serious damage in other parts of their introduced range (e.g. brook trout in northern Europe, Korsu *et al.* 2007, Spens *et al.* 2007).

Acknowledgements: Kristian Meissner helped with the meta-analysis. Jani Heino, Larry Greenberg and an anonymous referee provided helpful comments on an earlier version of the manuscript. Funding was provided by Maj and Tor Nessling Foundation, University of Oulu (Thule Institute) and the Academy of Finland.

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